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Seascape biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of benthic polychaetes

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ABSTRACT: The purpose of this paper is to investigate seascape biodiversity patterns along the Mediterranean and the Black Sea through the study of the benthic polychaete biogeography of the region. A set of non-parametric multivariate analyses and recently developed diversity indices were performed on the benthic polychaete inventories of the areas of the Mediterranean and the Black Sea. Both the numbers of species and the multivariate analyses demonstrate a west-east zoogeocline, shown by the decreasing number of species and by the multivariate similarity pattern of the areas. The performance of the 'second-stage' multi-dimensional scaling (MDS) shows, when species information is aggregated to genera, results belonging practically to the same similarity pattern, independent of the similarity coefficients utilized. The same similarity pattern is derived when species information is aggregated to the zoogeographical categories of amphi-Atlantic, Atlanto-Mediterranean, cosmopolitan and endemic species. BIO-ENV analysis reveals a large number of geographic, climatic and trophic variables to be highly correlated with the similarity pattern derived from the various taxonomic/zoogeographical categories. The synergy, however, of the environmental variables is best reflected in the case of the endemic Mediterranean species. The latter category is considered as the critical zoogeographic category with respect to providing information on the evolutionary history of the taxon in the region. The application of the average taxonomic distinctness and the variation of taxonomic distinctness indices resulted in a diversity ranking of the areas, which appears to be independent of the number of species hosted in each area. However, this is not the case for the phylogenetic diversity (PD) index. Additionally, the former 2 indices indicate that the benthic polychaete species-pool, hosted in the Mediterranean and the Black Sea areas, may well serve as a useful basis for future comparisons in environmental assessment studies. Finally, results from the application of the area-diversity formula show that the equilibrium model can be applicable for the endemic benthic polychaetes of the region: the number of endemic species can be considered as a function of the degree of isolation of the area from the source region against the degree of within-area isolated habitats.

KEY WORDS: Biodiversity · Biogeography · Polychaeta · Mediterranean · Black Sea

INTRODUCTION

Mediterranean marine biodiversity has received very little attention, despite its cultural and commercial significance for the surrounding countries. Bianchi & Mori (2000) give a rough estimation of the marine macroscopic species living in this sea, which ranges between 4 and 18% of the total of world marine species.

Previous attempts to assess the benthic macrofaunal diversity of the Mediterranean and the Black Sea have been focused almost exclusively on patterns deriving

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from numbers of species (e.g. Pérès & Picard 1958, Pérès 1967, Fredj 1974, Bacescu 1985 and references therein) and from the scientific efforts made in the region (e.g. Bellan-Santini 1985). These studies offered some evidence for the sole existing species diversity pattern: there is an eastward decline in species number. This pattern arguably still represents a hypothesis to be tested, as information on species distribution in the region is being accumulated.

Polychaeta is one of the richest invertebrate benthic groups in regard to species number, and has been traditionally considered as either the dominant group (in both abundance and biomass) or as an important contributor to the entire macrobenthic fauna (Fauchald 1977, Knox 1977). The importance of the taxon in community structure and environmental quality monitoring has been summarized in a number of publications (e.g. Pocklington & Wells 1992, Hutchings 1998). Significant effort has recently been made in the NE Atlantic regions, where hypotheses on quantitative patterns of species diversity have already been tested (e.g. Dauvin et al. 1994, Paterson & Lambshead 1995, Cosson-Sarradin et al. 1998, Paterson et al. 1998, Gillet & Dauvin 2000). However, in the Mediterranean and Black Sea regions, studies similar to those for the Atlantic regions have not been conducted.

In this paper, a series of non-parametric techniques was performed on benthic polychaete inventories of the Mediterranean and Black Sea areas. The aims were: (1) to search for seascape diversity patterns along the Mediterranean and the Black Seas in order to examine how the pattern changes as species are aggregated to higher taxonomic and zoogeographic categories as well as to investigate the environmental variables associated with them; (2) to test both the performance of various indices in the diversity ranking of the Mediterranean and Black Sea areas and the potential use of the taxon for future comparisons in environmental assessment studies; and (3) to examine the application of the area-diversity model in the region.

MATERIALS AND METHODS

Data. The Mediterranean and Black Sea areas considered in this study (Fig. 1) were adopted from Por (1989), with the exception of the Ionian Sea and the Sea of Sidra, which were considered as a single area: the Central Basin. Thus, the Mediterranean and Black Sea region is divided into 6 areas: Western Mediterranean, Central Basin, Adriatic Sea, Aegean Sea, Levantine Basin and Black Sea. These areas represent, in geomorphological terms, individual sub-basins, being separated from each other by straits and sills. Each of the 6 areas is considered as having a distinctive oceanographic regime: (1) the Western Mediterranean is characterized by its wide continental shelf, by lower salinity and temperature values as well as by higher primary productivity and chlorophyll *a* (chl *a*) concentration values than those occurring in the Eastern Mediterranean; (2) the Adriatic Sea, which has shallow waters, relatively low winter temperature values and low salinity is differentiated when compared to the other areas; (3) the Central Basin has high temperatures and is very deep in most of its largest part (Ionian Sea); (4) the Levantine Basin is characterized by great depths, high temperatures associated with high salinity values and oligotrophic conditions (low concentration

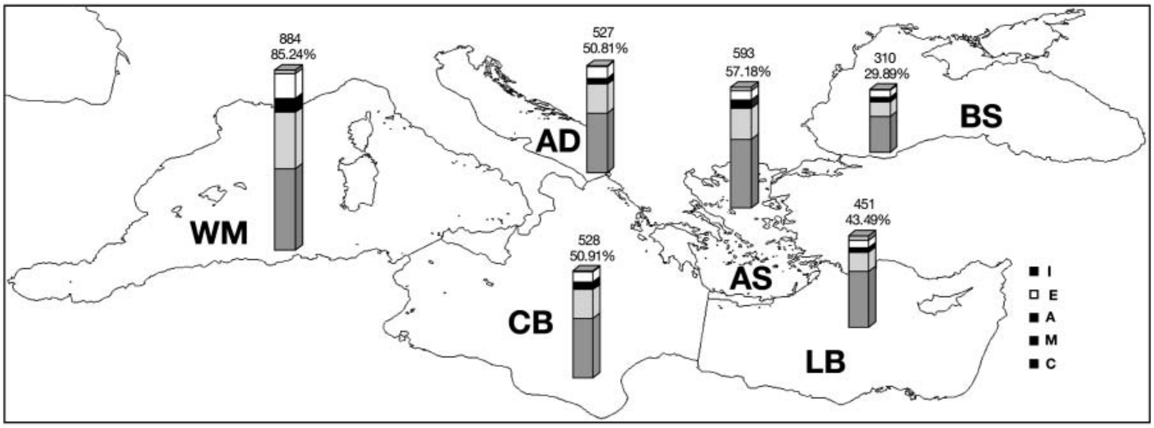

Fig. 1. Distribution of polychaete species in the main areas of the Mediterranean. Upper numbers are totals; lower, same numbers as percentages of the total Mediterranean species; distribution of the zoogeographical categories as percentages of the total number of species of each area indicated by different patterns of color on the bars. WM: Western Mediterranean; CB: Central Basin; AD: Adriatic Sea; AS: Aegean Sea; LB: Levantine Basin; BS: Black Sea; M: Atlanto-Mediterranean; A: amphi-Atlantic; C: cosmopolitan; E: endemic; I; Indo-Mediterranean

of nutrients); (5) the Aegean Sea, shallow in its largest part, has relatively low salinity and temperature values, and furthermore, is subject to the influx of the waters from the Black Sea; (6) the Black Sea is characterized mainly by reduced salinity and temperature as well as anoxic conditions. Information on the geomorphological and oceanographic conditions prevailing in the Mediterranean and Black Sea areas can be found in many studies such as Caspers (1957), Pérès (1967), Bacescu (1985), Fredj & Laubier (1985), Por (1989), Azov (1991), Psarra et al. (2000) and the references therein.

The distribution of the benthic polychaetes in the Mediterranean and Black Seas follows the one which is already registered on the ERMS webpage (www.erms.biol.soton.ac.uk). Classification and coding of the higher taxa follow the one suggested by Fauchald & Rouse (1997) and Rouse & Fauchald (1997).

Polychaete species were assigned to zoogeographical categories according to their distribution, as derived from the relevant literature: (1) species distributed only in the Mediterranean and the Black Seas have been considered as endemic; (2) species distributed in the Mediterranean and the eastern Atlantic have been considered as Atlanto-Mediterranean; (3) species distributed in the Mediterranean and both sides of the Atlantic have been considered as amphi-Atlantic; (4) species distributed in the Mediterranean and the Indo-Pacific have been considered as Indo-Mediterranean; (5) species distributed at least in the Atlantic, in the Mediterranean and in the Indo-Pacific have been considered as cosmopolitan.

Three categories of environmental variables were used during the study: geographic, climatic and trophic. The geographic variables include: (1) total surface area; (2) shelf surface; (3) distance of the area from the straits of Gibraltar; (4) distance from the Suez Canal; (5) insular surface; (6) number of islands; (7) average island distance from the nearest continent; and (8) average inter-island distance. These geographic variables were calculated using distance and area calculation functions in a geographic information system (GIS). A continuous World Vector Shoreline (1:250 000) for the Mediterranean and Black Seas was downloaded from the National Oceanic & Atmospheric Administration's (NOAA) National Geophysical Data Center website (rimmer.ngdc.noaa.gov/coast/getcoast.html) and the 200 m bathymetric contour was extracted through the Intergovernmental Oceanographic Commission's General Bathymetric Chart of the Oceans (GEBCO) digital atlas. Both data sets were introduced in Environmental Systems Research Institute's (ESRI) workstation ARC/INFO GIS (Valavanis et al. 1998). The method of on-screen digitizing was used to define the boundaries of the 6 divisions of the study area. The climatic variables include: (1) water column temperature, (2) salinity and (3) oxygen concentration. The trophic variables include: (1) phosphate, (2) nitrate and (3) silicate concentration. Both climatic and trophic variables were obtained from the objectively analyzed fields, which are included in the World Ocean Atlas (1994, National Oceanic and Atmospheric Administration, US Department of Commerce, National Oceanographic Data Center, Ocean Climate Laboratory, available at www.nodc.noaa.gov/OC5/pr_woa4.html).

In the analyses, average, maximum, minimum and range of values of the climatic and trophic variables were used.

Analyses. The Kruskal-Wallis test (Kruskal & Wallis 1952) was applied to assess any significant difference in the distribution of the zoogeographical categories, to which polychaete species have been assigned, in the areas considered.

An initial binary matrix was constructed where species' presence/absence in the Mediterranean and the Black Sea areas was marked as 1 or 0, respectively. The information included in the initial matrix was subsequently aggregated into the generic and family levels. Five additional matrices were also constructed in which the distribution of the species assigned to the 5 zoogeographical categories in the areas considered was recorded. To derive similarity patterns from the above matrices, 6 similarity coefficients were utilized: (1) Jaccard, (2) Sørensen, (3) Kulczynski, (4) Sokal & Sneath, (5) Ochiai and (6) Faith (see review by Legendre & Legendre 1998). The resulting similarity matrices were used for both cluster analysis (group-average linkage) and non-metric multidimensional scaling (nmMDS), as suggested by Field et al. (1982) and Clarke & Warwick (1994). The goodness-of-fit of the resulting 2-dimensional plots was measured using Kruskal's stress formula I (Kruskal & Wish 1978, Clarke & Green 1988). The significance of any differences found was determined by 1-way analysis of similarity (ANOSIM) randomization tests (Clarke 1993).

The resulting multivariate patterns were compared using the methods described by Somerfield & Clarke (1995). According to the mathematical procedure they describe, a rank correlation, using the harmonic rank correlation coefficient (Clarke & Ainsworth 1993), was computed between every pair of the 48 similarity matrices produced by the 8 taxonomic/zoogeographic levels and the 6 similarity coefficients. A final triangular similarity matrix was constructed with 1128 cells, containing the resulting values of the harmonic rank correlation coefficient. These correlation values were firstly ranked and subsequently subjected to the 'second stage' MDS (Olsgard et al. 1997).

The correlation between the multivariate patterns derived from the similarity matrices and the various combinations of the environmental variables was examined using the BIO-ENV analysis (Clarke & Ainsworth 1993).

The following recently developed diversity indices were used in order to compare the polychaete diversity of the Mediterranean and Black Sea areas: (1) average taxonomic distinctness (AvTD) as defined by Clarke & Warwick (1998), $\Delta^+ = [\sum\sum_{i<j}\omega_{ij}]/[s(s-1)/2]$, where ω_{ij} is the taxonomic path length between species i and j, and s is the number of species; (2) variation in taxonomic distinctness (VarTD) as defined by Clarke & Warwick (2001), $\Lambda^+ = [\{\sum\sum_{i<j}\omega_{ij}{}^2\}/\{s(s-1)/2\}] - [\Delta^+]^2$; and (3) phylogenetic diversity (PD) as defined by Faith (1992), i.e. the cumulative branch length of the full taxonomic tree. By constructing a simulation distribution (funnel) from random subsets of species from the regional polychaete inventory, both AvTD and VarTD statistics, calculated from the species lists of the areas considered, can be tested for departure from expectation (Clarke & Warwick 2001, Warwick & Clarke 2001). Values of AvTD and VarTD located within the 95% probability funnel mean that polychaete diversity in the corresponding areas falls within the expected range; hence, allowing both for sample-size sample-effort free diversity comparisons and for the use of the inventories in 'biological effects' monitoring studies in the future.

Two packages suitable for ecological analyses were used for the above-mentioned analyses: the R Package (Legendre & Vaudor 1991) and the PRIMER (Plymouth Routines In Marine Ecological Research) Package (Clarke & Gorley 2001).

Finally, the area-diversity formula $S = C \times A^z$, (MacArthur & Wilson 1963, 1967) was applied to test any significant relationship between the number of units included in every taxonomic/zoogeographic level and the geographic variables. In the formula, S represents the number of units, A the geographic variables and c and z are the intercept and slope of the regression. The first 2 of the geographic variables indicated in the data section are considered as indicative of the size of the area, the following 2 as indicative of the distance of the areas from the source region (Atlantic Ocean and Red Sea, in this case) and the last 3 variables are considered as indicative of the degree of within-area isolated habitats. Values of every pair of S and A were first transformed to logarithms (base 10) and a linear regression was subsequently performed (Zar 1999).

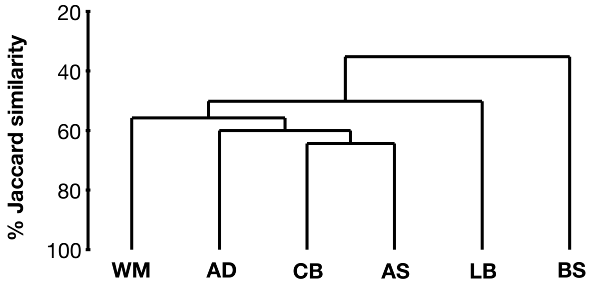

Fig. 2. Dendrogram resulting from the similarity matrix based on the Jaccard's coefficient. Area abbreviations as in Fig. 1

RESULTS

Polychaete fauna

Up to 1999, 1036 valid species of benthic polychaetes had been reported from the Mediterranean and the Black Seas. From these, 73 species were characterized as amphi-Atlantic, 297 as Atlanto-Mediterranean, 428 as cosmopolitan, 195 as endemic and 44 as Indo-Mediterranean. The number of species reported from the Mediterranean and Black Sea areas, and the percentages of the zoogeographical categories to which the species are assigned, are shown in Fig. 1. A decrease in the number of species from west to east is evident.

The polychaete fauna of the Western Mediterranean is considered as the best studied so far (884 species). Most of these species (402) are characterized as cosmopolitan, 275 as Atlanto-Mediterranean, 68 as amphi-Atlantic, 121 endemic and 18 Indo-Mediterranean. A total of 528 species has been reported from the Central Basin. The distribution of the polychaete species in the zoogeographical categories is: 291 cosmopolitan, 143 Atlanto-Mediterranean, 37 amphi-Atlantic, 50 endemic and 7 Indo-Mediterranean. The Adriatic Sea hosts 527 species, of which cosmopolitan is again the major category, followed by Atlanto-Mediterranean, amphi-Atlantic, endemic and Indo-Mediterranean. According to the literature, 593 species are known from the Aegean Sea. Cosmopolitan species come first containing 336 species, followed by Atlanto-Mediterranean, endemic, amphi-Atlantic and Indo-Mediterranean species. The Levantine Basin is the second most impoverished area in species richness, hosting a total of 451 species. The ranking of the zoogeographical categories is as in the Western Mediterranean (Fig. 1). It should be noted that the number of species with Indo-Mediterranean distribution reported from the Levantine Basin is the highest of the Mediterranean areas considered in this study. The Black Sea is the most impoverished of the areas taken into account (310 species) with the zoogeographic categories ranked similarly as in the Aegean Sea.

The distribution of the zoogeograhical categories does not appear to be different among the areas considered in this study. The Kruskal-Wallis test performed on the above numbers gave the value of 1.9 for the statistic $H_{(5,\,30)}$ ($p \gg 0.05$).

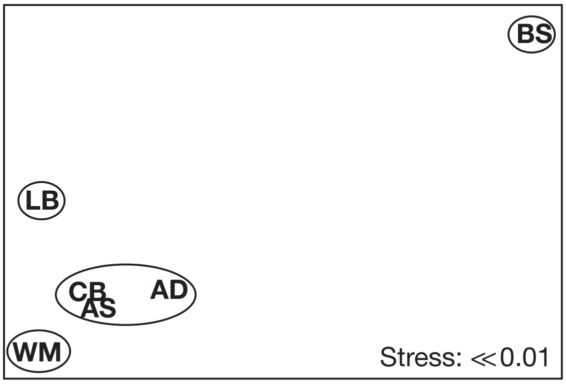

Fig. 3. Non-metric multidimensional scaling (nmMDS) ordination plot resulting from the similarity matrix based on Jaccard's coefficient. Area abbreviations as in Fig. 1

Multivariate pattern

The dendrogram resulting from the similarity matrix based on Jaccard's coefficient is presented in Fig. 2. The Aegean Sea, Central Basin and Adriatic Sea areas form the first group with high similarity (60.03%). The Western Mediterranean forms the second one and joins this group at the level of 55.75%, while the Levantine Basin and Black Sea areas (third and fourth groups, respectively) are added at lower similarity levels (50.16 and 35.2%, correspondingly). The ANOSIM test gave the value of 0.944 for the Global R ($p < 0.05$), which indicates that the previously identified groups seem to be significantly different. Based on the same similarity matrix as the dendrogram, the MDS plot (Fig. 2) shows the same trend but maximizes the distances between the areas of the Mediterranean and Black Seas.

Each matrix deriving from taxonomic/zoogeographic levels was subjected to different similarity coefficients. Rather than presenting the resulting 48 MDS plots for comparison, the 'second-stage' MDS procedure was adopted. The output plot of the latter analysis where similarity matrices with similar configuration are plotted close to each other is shown in Fig. 4. The most distant groups in the plot include the matrices resulting from the taxonomic level of family (Group B) and the zoogeographic level of Indo-Mediterraneans (Groups C and D). Two other distinct groups appear, namely Groups E and F, proximal to the larger Group A, which represent matrices for the zoogeographical groups of the Atlanto-Mediterranean and endemic species analyzed by Kulczynski's coefficient (the former) and by the Faith's coefficient (the latter). The matrices resulting from the remaining taxonomic/zoogeographic levels lie close to each other, within the larger Group A.

Associated environmental variables

A summary of the results from the BIO-ENV analysis is given in Table 1. Similarity matrices derived from the lower taxonomic levels (species, genus) are most highly correlated with maximum values of oxygen. In the case of the species similarity matrices as calculated by the Kulczisnky and the Faith coefficients, distance from both Gibraltar and Suez as well as phosphate concentration are also added to the associated environmental variables. An almost identical correlation pattern is derived from the matrices with the amphi-Atlantic and Atlanto-Mediterranean species.

Matrices derived from the family level are highly correlated with distance from Gibraltar, distance from the Suez Canal, average values of oxygen and silicate concentration. This pattern remains almost unchanged, no matter which coefficient is used.

In the case of the endemic Mediterranean species, the following set of the environmental variables appears to be best correlated with the corresponding similarity matrices, i.e. distance from both Gibraltar and Suez, maximum values of oxygen concentration and phosphate concentration (maximum values). Deviations from the above variables are seen only when Faith's coefficient is used.

The multivariate pattern deriving from the category of the cosmopolitan species is best correlated with the highest number of environmental variables, which include distance from both Gibraltar and Suez, average distance of islands from the nearest continent, range of temperature, salinity and oxygen concentration values, and average phosphate concentration val-

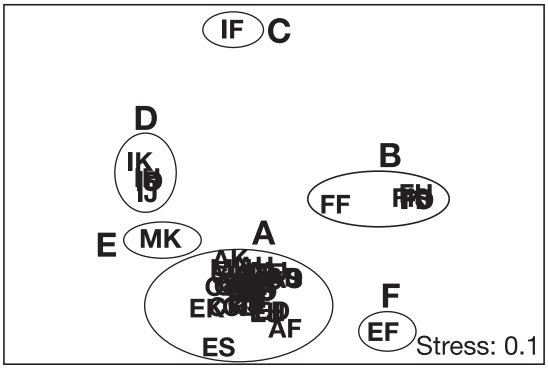

Fig. 4. 'Second-stage' ordinations by nmMDS of ranked inter-matrix correlations. First letter in each pair corresponds to the taxonomic/zoogeographic categories (S: species; G: genus; F: family; zoogeographic categories as in Fig. 1); second letter indicates the similarity coefficient used (J: Jaccard's; D: Sørensen's; K: Kulczynski's; S: Sokal & Sneath's; H: Ochiai's; F: Faith's); letters A to F near circles indicate groups of highly correlated matrices

Table 1. Environmental variables, best correlated with the distribution pattern of the benthic polychaetes in the Mediterranean and Black Sea areas DSGL: distance from Gibraltar; DSSZ: distance from Suez; DSCN: average island distance from the nearest continent; NBIS: number of islands; TMRN: range of temperature values; SLMN: minimum salinity values; SLRN: range of salinity values; OXMX: oxygen concentration maximum values; OXAV: average oxygen concentration values; OXRN: range of oxygen concentration values; PHMX: phosphate concentration maximum values; PHAV: average phosphate concentration values; SIMX: silicate concentration maximum values; SIMN: silicate concentration minimum values; ρ_w: harmonic rank coefficient. Abbreviations in first column given in Fig. 4 legend

	Environmental variables														
	DSGL	DSSZ	DSCN	NBIS	TMRN	SLMN	SLRN	OXMX	OXAV	OXRN	PHMX	PHAV	SIMX	SIMN	ρ_w
Species															
SJ								+							0.83
SD								+							0.83
SK		+						+				+			0.74
SS								+							0.83
SO								+							0.78
SF	+	+						+				+			0.77
Genus															
GJ								+							0.77
GD								+							0.77
GK								+							0.72
GS								+							0.77
GO								+							0.77
GF		+						+							0.63
Family															
FJ		+	+						+				+		0.86
FD		+	+						+				+		0.86
FK		+	+						+				+		0.85
FS		+	+						+				+		0.86
FO		+	+						+				+		0.84
FF		+											+		0.91
Amphi-atlantic															
AJ								+							0.73
AD								+							0.73
AK		+						+							0.73
AS								+							0.73
AO								+							0.67
AF								+							0.66
Atlanto-mediterranean															
MJ								+							0.83
MD								+							0.83
MK	+	+						+							0.57
MS								+							0.83
MO	+	+						+							0.7
MF								+							0.75
Cosmopolitan															
CJ		+	+		+		+					+			0.71
CD	+	+			+		+					+			0.68
CK		+			+					+					0.72
CS		+	+		+		+					+			0.71
CO		+	+		+		+					+			0.71
CF					+		+			+					0.73
Endemic															
EJ	+	+						+			+				0.9
ED	+	+						+			+				0.9
EK	+	+						+			+				0.64
ES	+	+						+			+				0.78
EO	+	+						+			+				0.85
EF	+	+	+								+		+		0.92
Indo-Mediterranean															
IJ						+								+	0.88
ID						+								+	0.86
IK						+								+	0.81
IS						+								+	0.86
IO						+								+	0.84
IF		+		+											0.81

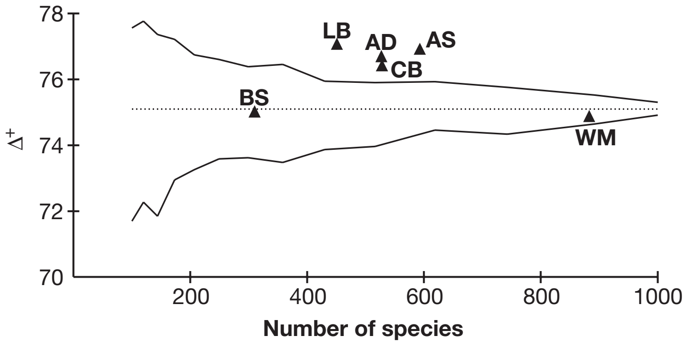

Fig. 5. The 95% probability funnel for the average taxonomic distinctness values. Expected average indicated by the straight line in the middle of the funnel. Area abbreviations as in Fig. 1

ues. Different combinations of the above variables are correlated when different similarity coefficients are used.

Minimum values of salinity and silicate concentration are highly correlated with the matrices derived from the Indo-Mediterranean species, except in the case where Faith's coefficient is used. In this case, distance from Suez and number of islands are the most highly associated variables.

Polychaete diversity

The 95% funnel for the simulated distribution of average taxonomic distinctness (Δ^+) for random subsets of fixed species number from the Mediterranean and Black Seas' polychaete species list is displayed in Fig. 5. Superimposed on this funnel are the estimated values of Δ^+, resulting from the species lists from the 6 areas of the Mediterranean and Black Seas. For the Black Sea and the Western Mediterranean, the calculated Δ^+ values of 75.01 and 74.88, respectively, were close to the expected mode of the funnel, according to the number of species they host. For the remaining areas, Central Basin, Adriatic Sea, Aegean Sea and Levantine Basin, Δ^+ values were 76.41, 76.69, 76.91 and 77.07, respectively. These values are beyond the upper limit of the simulated distribution under the null hypothesis, and there is a significant departure at the 2% level ($p < 0.02$) in all cases.

Similarly, the 95% funnel of the variation in taxonomic distinctness (Λ^+) from the Mediterranean and the Black Sea areas is shown in Fig. 6. Here, the Central Basin and the Western Mediterranean have Λ^+ values close to the lower limit the former (380.6) and to the higher limit the latter (407.4), but in neither case is there a significant departure from the null hypothesis ($p > 0.05$). All of the remaining areas have Λ^+ values close to the expected simulated mode of the funnel.

Spearman's rank correlation coefficient performed between the values of the indices as calculated for the above 6 areas gave no significant results ($\rho < 0.2$, $p > 0.6$), indicating that the above indices act independently of each other and, perhaps, add some new information to the study.

The calculated values of the PD index are 33.6×10^3 for the Western Mediterranean, 24×10^3 for the Aegean, 22.2×10^3 for both the Central Basin and Adriatic, 19.2×10^3 for the Levantine Basin and 14×10^3 for the Black Sea (Fig. 7). The PD values rank the areas differently from the above 2 indices. Values of the PD index seem to be significantly correlated with the number of species.

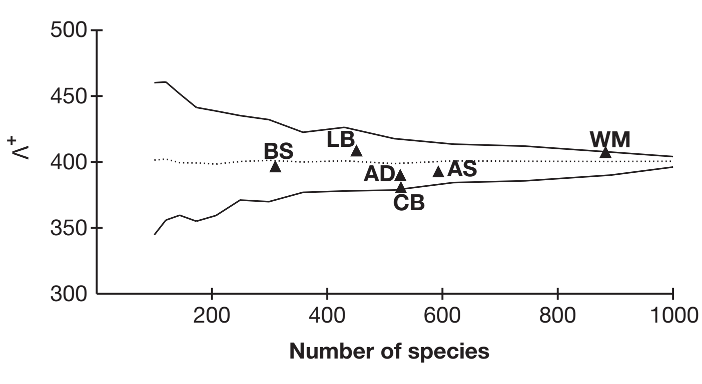

Fig. 6. The 95% probability funnel for the variation in taxonomic distinctness values. Expected average indicated by the straight line in the middle of the funnel. Area abbreviations as in Fig. 1

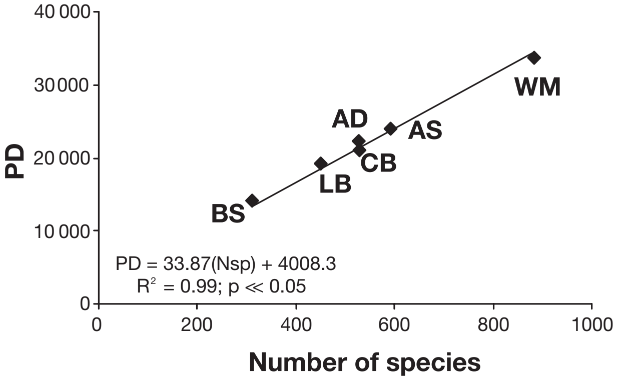

Fig. 7. The average phylogenetic diversity values (Φ^+), plotted against the number of species, hosted in each area. The linear relationship between Φ^+ values and the number of species (NSp) is indicated by the regression fitted, at the bottom of the plot. Area abbreviations as in Fig. 1

Table 2. Summary of the regression results of the formula applied: $S = C \times A^z$, where S represents the number of taxonomic/zoogeographic units (coding as in Figs. 1 & 7) and A represents the value of the indicated geographic variables. S: species; G: genera; F: family; A: amphi-Atlantic; M: Atlanto-Mediterranean; C: cosmoplitan; E: endemic; I: Indo-Mediterranean

	S	G	F	A	M	C	E	I
Total surface								
r^2	0.28	0.27	0.47	0.3	0.45	0.15	0.46	0.12
p-value	0.27	0.28	0.13	0.25	0.14	0.44	0.13	0.48
Intercept	1.76	1.77	1.38	0.79	0.092	1.9	0.13	−0.15
Slope	0.16	0.15	0.06	0.22	0.24	0.092	0.26	0.19
Insular surface								
r^2	**0.92**	**0.93**	0.59	**0.82**	0.63	**0.93**	**0.69**	0.42
p-value	0.002	0.001	0.074	0.011	0.057	0.001	0.04	0.16
Intercept	2.16	2.15	1.61	1.41	0.97	2.01	1.09	0.32
Slope	**0.14**	**0.14**	0.033	**0.18**	0.14	**0.11**	**0.16**	0.18
Shelf surface								
r^2	0.3	0.29	0.59	0.38	0.62	0.13	0.59	0.014
p-value	0.25	0.26	0.071	0.18	0.061	0.47	0.072	0.82
Intercept	1.56	1.58	1.27	0.38	−0.44	1.85	−0.37	0.55
Slope	0.2	0.2	0.084	0.31	0.35	0.1	0.37	0.083
Average island distance from continent								
r^2	**0.87**	**0.88**	0.49	**0.76**	0.61	**0.88**	0.61	0.54
p-value	0.006	0.005	0.12	0.022	0.065	0.004	0.065	0.093
Intercept	2.32	2.3	1.65	1.62	1.12	2.13	1.28	0.43
Slope	**0.3**	**0.31**	0.068	**0.39**	0.31	**0.24**	0.34	0.45
Average among islands distance								
r^2	0.003	0.002	0.015	0.001	0.032	0.001	0.014	0.14
p-value	0.91	0.91	0.81	0.93	0.73	0.95	0.81	0.45
Intercept	2.62	2.61	1.68	2.03	1.15	2.5	1.44	−0.2
Slope	0.041	0.041	0.027	0.041	0.16	−0.019	0.12	0.53
Distance from Gibraltar								
r^2	0.61	0.59	**0.8**	0.62	**0.73**	0.4	**0.85**	0.16
p-value	0.066	0.071	0.014	0.06	0.029	0.17	0.008	0.41
Intercept	2.95	2.94	1.82	2.45	1.84	2.61	2.08	1.25
Slope	−0.087	−0.085	**−0.03**	−0.11	**−0.11**	−0.056	**−0.13**	−0.085
Distance from Suez								
r^2	0.055	0.046	0.18	0.14	0.29	0.009	0.18	0.32
p-value	0.65	0.68	0.39	0.46	0.26	0.85	0.39	0.23
Intercept	2.64	2.64	1.7	1.97	1.33	2.43	1.55	1.33
Slope	0.028	0.026	0.015	0.061	0.07	0.009	0.067	−0.12

Application of the island biogeography formula

Results derived from the application of the area-diversity formula are displayed in Table 2. Significant results are derived in the following cases: (1) when A is the insular surface and S represents the number of species, genera, and number of amphi-Atlantic, cosmopolitan and endemic species; (2) when A is considered to be the average island distance from the continent and S is again the number of species, genera, amphi-Atlantic and cosmopolitan species; (3) when A represents the distance from Gibraltar, and S represents the number of families and the number of Atlanto-Mediterranean and endemic Mediterranean species. In the first case, the parameter z takes values between 0.11 and 0.18, in the second case values between 0.24 and 0.39 and in the third case, z takes negative values between −0.13 and −0.03.

DISCUSSION

The zoogeocline

Bellan (1991) estimated the number of the benthic polychaetes in the Mediterranean as up to 950 species, classified into 71 families. The polychaete species known to be distributed in the Mediterranean and Black Seas belong to 392 genera and 66 families. The number of higher categories has been substantially reduced recently as a result of the phylogenetic analysis of the group (Fauchald & Rouse 1997, Rouse & Fauchald 1997). Furthermore, application of the phylogenetic principles on the polychaete systematics has resulted in questioning the usefulness even of the Linnaean system (Sundberg & Pleijel 1994, Rouse & Fauchald 1997).

Based on the number of species hosted in each area, a west-east gradient with decreasing values can be observed, with 1 exception: the Aegean Sea. Arvanitidis (1994, 2000) states that although the Aegean Sea has not been studied so well and is located farther from Gibraltar than other areas (Central Basin, Adriatic Sea), it is classified as second in species richness after the Western Mediterranean. However, the eastward decline of species number of the total macrobenthic fauna has already been stated in a number of publications (e.g. Pérès & Picard 1958, Bacescu 1985).

Both cluster analysis and MDS reveal a clear pattern, which cannot be derived either from the taxonomic distinctness indices applied or from the distribution of the zoogeographical categories in the areas considered. In the MDS plot, the groups are arranged along a west-east gradient, henceforward termed as the zoogeocline, corresponding to the species number they host. An eastward negative gradient in species richness has also been observed from the study of marine species of current or potential interest to fisheries (Garibaldi & Caddy 1998).

Patterns from aggregated information

Results derived from the 'second-stage' MDS show that the similarity pattern remains practically unchanged from the specific to the generic taxonomic level and in the matrices deriving from the amphi-Atlantic, Atlanto-Mediterranean, cosmopolitan and endemic species, in the cases where the similarity coefficients of Jaccard, Sørensen, Sokal & Sneath, and Ochiai are used. However, in the cases where the coefficients of Kulczynski and of Faith are used, there may be some deviations from the pattern. The above results at the taxonomic level may be interpreted as a result of the likely evolutionary history of the Mediterranean and Black Seas' fauna: marine species, and among them polychaetes, have colonized and enriched the Mediterranean mainly from the Atlantic through the Gibraltar Straits and have had the evolutionary time to acclimatize and evolve. Over the last 5 million years (late Pliocene-Peistocene; Por 1989, Briggs 1996), they have adapted to an extreme diversity of habitats offered to them by this regional sea and have accumulated in greater numbers than in the Altantic waters located in the vicinity of the Mediterranean (e.g. Bacescu 1985, Bellan-Santini 1985). Thus, at the present time, the number of genera to which species reported from this regional Sea belong is more than 25% the total number of species. The latter implies that no matter what the unevenness of the distribution of species within the genera, the information accumulated in the generic taxonomic level is sufficient to produce the same pattern as the one produced by the specific level. However, this is not the case with the higher taxonomic levels. A number of mono- or oligo-specific families occurring only in some of the areas may well cause a substantially altered similarity pattern. When information is aggregated into orders, as defined by Fauchald (1977) and Pettibone (1982), the analysis also results in different patterns (not shown).

Synergy of environmental factors

Plausible explanations can be offered for all the environmental variables best correlated with the multivariate distribution pattern of the polychaetes in the Mediterranean and Black Seas (e.g. Bellan 1964, Day 1967, Reish 1979). These variables may be divided into 2 categories: (1) variables reflecting different aspects of the degree of the isolation of the habitats in the areas considered (distance of the area from both Gibraltar and Suez, average island distance from the nearest continent and number of islands); and (2) variables reflecting the degree of adaptation of the species to the environmental constrains occurring in the Mediterranean and Black Sea areas (temperature, salinity, oxygen availability, phosphate and silicate concentration). Taking into account the relatively short but eventful geological history of the Mediterranean and Black Seas, however, all the above variables should be considered as offering no more than an indication of what is likely to have happened to species distribution patterns, with the exception of the geographic variables. It is worthwhile mentioning that the few main environmental variables correlated with the pattern derived from similarity matrices produced by the species, genera, and amphi-Atlantic and Atlanto-Mediterranean species, are almost identical. However, more variables are added when the pattern was derived from matrices produced by families, and cosmopolitan and endemic species.

Cosmopolitan polychaete species appear to be the most abundant zoogeographical category in the Mediterranean and Black Seas, comprising more than 30% of the total number of species. High percentages of polychaete species with cosmopolitan distribution have been commonly observed in many parts of the world (e.g. Fauvel 1923, Bellan 1964, Day 1967). Species with cosmopolitan distribution are considered to be euryoecious and frequently opportunistic species, and their populations are considered to be capable of colonizing different types of habitats by developing a variety of adaptations in order to survive in different environments, especially in coastal waters (Grassle & Grassle 1974, Pearson & Rosenberg 1978). The development of these adaptations determines their distribution pattern in the areas considered. The latter may explain, to a certain degree, the number of environmental variables best correlated with the similarity pattern derived from this category of species. However, the issue of the widely distributed polychaete species has been discussed in a number of studies (e.g. Fauchald 1984, Williams 1984, Mackie & Hartley 1990, Dauvin & Thiébaut 1994), where it was shown that, at least for a number of names used to classify certain species considered to have world-wide distribution (e.g. *Terebellides stroemi*, *Prionospio ehlersi*, *Spio filicornis*), several different species from various areas of the world had, in fact, been included. In Australia, where most terebellids had been suffering from the 'cosmopolitan syndrome', it was shown that these species had not been correctly identified in the past. It is anticipated that a similar pattern will be found in South America and New Zealand (Hutchings 1998). Since most of the species occurring in the Mediterranean and Black Seas have been described from these seas or from the NE Atlantic, it is anticipated that with a further accumulation of evidence resolving the 'cosmopolitan syndrome', polychaete species assigned to this category of species will be, at least partly, removed to the categories of amphi-Atlantics or endemics.

The synergy, however, of the 3 categories of the environmental variables—geographic, climatic and trophic—is best reflected in the case of the endemic Mediterranean species, where the highest ρ_w values occur. The first variable is an expression of the distance of the areas from the main source of species (Atlantic Ocean). The second variable expresses the distance from the Suez Canal and ranks the areas in the reverse order, with the exception of the Black Sea. According to this variable the Black Sea is ranked third, whereas according to the former variable this area is ranked sixth. The latter is indicative of a potential source of species, proximal to the Black Sea. The only evidence that can offer a plausible explanation for the existence of such a source of species is the presence of some species, regarded as having originated from the Sarmatian and Pontian Sea (Briggs 1996). Five species distributed in the Ponto-Caspian Basins (exclusively endemic to this area) can be included in this category: *Hypania brevispinis* (Grim in Grube, 1860), *Hypania invalida* (Grube, 1860), *Hypania kowalewskii* (Grim in Grube, 1887) *Fabricia stellaris caspica* (Zenkevitch, 1922) and *Manayunkia caspica* (Annenkova, 1929). Oxygen availability could be interpreted as a limiting factor mainly for the Black Sea (Caspers 1957), where anoxic conditions prevail from 150 to 200 m and deeper, and associated with the higher temperature, could be considered as a limiting factor for the Levantine Basin. Phosphate concentration, on the other hand, has been considered as an expression of the oligotrophic conditions prevailing in the Eastern Mediterranean (Por 1989). The high percentage of the endemic species in the Mediterranean and the Black Seas, which approaches 20% in the case of benthic polychaetes, can be interpreted as a result of 2 factors: (1) the eventful geological history of the region, which has led to an important diversification of habitats; and (2) the diversity in the origin of the species (boreal, temperate, tropical, Sarmatic-Pontocaspian), which have either colonized the Mediterranean Sea after its last re-opening or remained as relicts in the Black Sea (Bellan-Santini 1985, Tortonese 1985, Bianchi & Mori 2000). The most meaningful conclusion, i.e. the one that best fits the compelling accumulation of evidence presented above, is that the evolutionary history of the taxon in the Mediterranean and Black Seas could be derived from the detailed study of this category.

For the cases of the matrices derived from the family and the Indo-Mediterranean level, the environmental variables found to be best correlated were quite different. This, however, is considered to result from the fact that the multivariate pattern derived from the family level is caused primarily by the inclusion of some families, which have hardly ever been recorded.

In the case of species with Indo-Mediterranean distribution, salinity and silicate concentration were found to be the best correlated variables. The correlation of salinity with the similarity pattern of the Indo-Mediterranean species is a rather predictable result since species migrating to the Levantine Basin had to encounter the salinity barrier of the Bitter Lakes (Por 1978). Recently, the salinity in the Suez Canal has dropped to 41‰, which is not very different from the salinity values measured in the SE Mediterranean or the Red Sea (Briggs 1996). On the occasion when the coefficient of Faith was utilized, both distance from the Suez Canal and the number of islands were best correlated with the pattern of the species of this category, demonstrating the significance of the degree of isolation from the source of migrating species, which complies in all aspects with the pattern of the migration as expressed by Por (1978, 1989, 1990).

Ranking biodiversity of Mediterranean and Black Seas

According to the Δ^+ values, all of the areas of the Mediterranean and the Black Seas are as diverse as expected (expectation refers to the values produced by simulation and located in the funnel) or even higher than expected. The Black Sea and Western Mediterranean areas belong to the first category and the Central Basin, the Adriatic, the Aegean Sea and the Levantine Basin to the second. This can be explained if one takes into account the way in which the average taxonomic distinctness is calculated: it focuses not only on the length of the phylogenetic tree, which mainly concentrates on the diversity of the higher taxa, but also on the evenness, which counts for the distribution of the lower taxa (species in this case) in the higher ones. Thus, in the Western Mediterranean is not only the number of the recorded species higher, but the higher taxa also include more species than in the remaining areas. In the remaining areas, genera, families or even higher mono- and oligo-specific taxa commonly occur. Consequently, the evenness component of the index can explain the higher than expected values for the 4 areas of the second category. The same evenness component seems to increase eastwards, from the Central Basin to the Levantine Basin, and it may offer a complete explanation of the ranking of the areas. The eastward increasing evenness component may reflect, up to a certain degree, the existing scientific expertise in the areas considered, with the Western Mediterranean being first in order (e.g. Bellan-Santini 1985). In the case of the Black Sea, however, the value of Δ^+ can be explained as a result of the considerably lower number of species reported from this area (almost 25% of the total species-pool of the entire region). This results in the reduction of the total length of the tree by the absence of a number of higher taxa combined with the number of species recorded in this area.

Values of the variation in the taxonomic distinctness index are located in the funnel with the expected values produced by the simulation procedure. This means that in each area, the average number of species included in the higher taxa, for each set of species specified at each step of the simulation procedure, remains relatively stable. It also means that the previously discussed Δ^+ values fall within the expected range of variability, as calculated for each area.

Following the terminology of Faith (1992, 1994) and Humphries et al. (1995), the PD index focuses exclusively on the 'character richness' rather than on the 'character combinations'. This means that the index concentrates on taxon richness and ignores the evenness component of the diversity, as observed by Clarke & Warwick (1998). The total branch length of the full taxonomic tree increases each time a species is added. As a result of the above properties, the ranking of the PD values calculated from the Mediterranean and Black Sea areas depends on the number of species they host. Clarke & Warwick (2001) have applied the PD index in species lists of free-living nematode assemblages from the British Isles and also found the index to be highly dependent on species numbers. Consequently, the utility of the PD index in those kinds of analyses based exclusively on the species lists appears to be questionable.

Basis for future comparisons

Warwick & Clarke (1998) and Clarke & Warwick (2001) applied the Δ^+ and Λ^+ to data derived from free-living marine nematodes found in both degraded and non-degraded locations around the British Isles. Both indices provided evidence for a loss of biodiversity in locations affected by various kinds of anthropogenic disturbance. In the present study, both indices indicate that using the benthic polychaetes as the indicator taxon does not suggest any severe degradation of the areas considered as a whole, when the polychaete fauna present is assumed to be in a natural state. The previously discussed results show that the species lists could serve as the basis, i.e. starting point or 'norm', for future comparisons. Subsequent use of the indices, in locations where the effects of the anthropogenic activities have been detected (e.g. Boudouresque et al. 1994, Ribera et al. 1996, Zaitsev & Mamaev 1997, Mee & Topping 1999, Perez et al. 2000), should be performed in order to reveal any loss trend in local biodiversity. Nevertheless, it should be kept in mind that polychaetes, as well as the meiobenthic nematodes (Pearson & Rosenberg 1978, Warwick & Clarke 1993), are the most resilient taxa in the benthic environment, where stress from anthropogenic activities is observed.

Towards the equilibrium model

MacArthur & Wilson (1967) state that the main relation between the area size and species number exists not only for island faunas, but also for non-isolated faunas such as the faunas within islands or within continents. An attempt was made during the present study to relate the number of taxonomic and zoogeographic units not only with the total surface of the areas considered, but also with other measures of the degree of isolation of the areas from the source of species and the degree of within-area habitat isolation. The application of the formula demonstrated the important role of some geographic variables such as the insular surface and the average island distance from the nearest continent. The insular surface, however, was never entered in the BIO-ENV analysis as highly correlated, while the average island distance from the nearest continent was never correlated with the pattern derived from the specific and generic level. Surprisingly, distance from Gibraltar was never correlated with the pattern derived from the family matrix. The differences resulting from the 2 methods can be caused by 2 factors: (1) the fact that their mathematical approach is different in that the formula relates numbers with numbers, while BIO-ENV correlates patterns derived from various taxonomic/zoogeographic levels with patterns derived from values of environmental variables; and (2) the fact that the number of observations, each time the formula is applied, was very low (relation derived from 6 pairs of values). Nevertheless, although the BIO-ENV analysis could be considered as more sensitive in that it permits more than 1 environmental variable to enter into the analysis, the species-area model can also give meaningful results. The species-area model produced realistic numbers in the case of the endemic species, the number of which was found to be positively related with the insular surface and negatively related to the distance of the area from the source region.

The equilibrium model (MacArthur & Wilson 1963) predicts the logarithm of the number of species as a function of immigration against extinction rates. Bouchet & Taviani (1992) demonstrated that the equilibrium model could be applied to the deep Mediterranean: molluscan populations in the deep basins are the result of equilibrium between larval influx (immigration) from the Atlantic and incapacity to settle or to reproduce (extinction). Based on the above, the equilibrium model as such is potentially applicable to the endemic benthic Polychaeta of the Mediterranean and the Black Seas; assuming that the migration and extinction rates are within the expected range, numbers of the endemic species (in logarithms) can be considered as the result of equilibrium between the degree of isolation of the area from the source regions and the extent of the isolation of the habitats within the areas.

CONCLUDING REMARKS

To summarize, the following conclusions can be drawn: (1) A west-east zoogeocline, with decreasing numbers of benthic polychaete species, is present throughout the Mediterranean and the Black Seas. A similar gradient can be observed from the multivariate similarity pattern of the areas. (2) The performance of the 'second-stage' MDS indicates that information on the species or genera distribution results practically in the same similarity pattern, independently of the similarity indices utilized. The same similarity pattern is evident when information on species distribution is aggregated to the zoogeographical categories of amphi-Atlantic, Atlanto-Mediterranean, cosmopolitan and endemic species. (3) A large number of environmental variables highly correlated with the multivariate pattern derived from the various taxonomic/zoogeographical categories can be found. (4) The category of the endemic species should be considered as the critical zoogeographic category in providing information on the evolutionary history of the taxon in the region. (5) Various diversity indices rank the Mediterranean and the Black Sea areas differently. The application of the average taxonomic distinctness and the variation of taxonomic distinctness indices resulted in a diversity ranking of the areas, which seem to be sample-size and sample-effort free. This is not the case for the PD index. (6) The benthic polychaete species-pool, reported from the Mediterranean and the Black Sea areas, may well serve as a useful basis for future comparisons in environmental assessment studies. And (7) The equilibrium model is probably applicable for the endemic benthic polychaetes of the region: the number of endemic species can be considered as a function of the degree of isolation of the area from the source region against the within-area isolated habitats.

Although the new biodiversity information provided here is based on the benthic polychaetes, it represents an improvement over the information that is currently available, particularly for the taxon. Clearly, further theoretical and perhaps computational advances in dealing with data deriving not only from a single taxon but also from the total of the macrobenthic fauna are required; this falls outside the scope of the present paper. Nonetheless, this biodiversity information offers a basis for future comparisons.

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